BIOLOGY AND IMMATURE STAGES OF *SETACERA NEEDHAMI* JOHANNSEN (DIPTERA: EPHYDRIDAE)[1,2]

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Abstract.—Adults of *Setacera needhami* Johannsen are common on algal mats from late March or early April until late May, and again during August and September. The period of aestivation, from June through early August, is spent in the pupal stage. Overwintering occurs in the adult and pupal (possibly pharate adult) stages. Larvae are common throughout the same periods as adults except during the winter at which time they are not found. Mating and oviposition takes place on the algal mats. Egg to adult development time ranges from 15 to 26 days. The species probably undergoes two to three generations by June and may accomplish two more during the late summer and fall. Extended periods of rain and/or cold may serve to regulate population levels, especially during the spring. Pedators include dolichopodid flies, dragonfly naiads, and surface-feeding ducks, among others. The egg, three larval instars, and puparium are described and illustrated using line drawings and scanning electron micrographs.

The genus *Setacera* is represented by eight New World species, seven of which occur in the United States. Most are western in distribution with only two, *Setacera atrovirens* (Loew), which occurs trans-boreally and throughout the midwestern states, and *S. pilicornis* (Coquillett), which is found in Florida, populating the eastern half of the United States (Mathis, 1982). Few biological studies have been conducted on members of the genus.

Sturtevant and Wheeler (1954), in their synopsis of the Nearctic Ephydridae, stated that most of their observations placed *Setacera* in freshwater habitats that had still or rather slow-moving water. In addition, they discussed the characteristic flight pattern of the genus, and Ephydrini in general, in which the adults rarely fly more than a small distance perpendicular to the surface of the water while traveling a considerable distance from the shore. They speculated that this may be one reason why specimens of *Setacera* are relatively rare in collections.

Setacera needhami Johannsen is confined to the far western United States, with specimens being recorded from Arizona, California, Utah, Nevada, Oregon, and Washington (Mathis, 1982). This species is relatively easy to separate from its

North American congeners, two of which, *S. aldrichi* Cresson and *S. pacifica* (Cresson), are often found sympatrically with *S. needhami* in Washington State localities. Separation of these three species is accomplished by using the length of the dorsal slope of the facial prominence which is longer than its height in *S. aldrichi* and by the lack of a papilla-like prominence on the supraspiracular convexity which occurs in *S. pacifica* but not in *S. needhami*. For a more thorough examination of the taxonomy of this group one should consult the revision of *Setacera* by Mathis (1982).

The designation of the specific name *needhami* is unusual, in that through a misunderstanding it was first described from the immature forms. Johannsen, in preparing for his treatise on aquatic Diptera (Johannsen, 1934, 1935, 1937a, 1937b), had sent adult specimens of *S. needhami*, which he reared, to Ezra T. Cresson, Jr. for determination. Cresson, not realizing that these determinations were to be used in a forthcoming publication, neglected to inform Johannsen that *S. needhami* was a manuscript name. Thus, when first published (Johannsen, 1935) the name *S. needhami* was based on a description of the third larval instar and puparium.

Biological data concerning both adult and immature stages of *S. needhami* are lacking. Johannsen (1935) sketchily described the third larval instar and the puparium of *S. needhami*, as well as the puparium of *S. atrovirens*. In addition, he figured the cephalopharyngeal skeleton of the third larval instar of *S. needhami*. His biological data concerning the species were limited to a recorded rearing from Laguna Beach, California.

Studies related in this paper were conducted in and around the Columbia National Wildlife Refuge (Grant and Adams counties) of east-central Washington. Although the species was occasionally collected at other localities throughout Washington and Oregon, nowhere was it found in such abundance as in the Refuge. Techniques used in this study were the same as those described by Zack (1982, *in press*) in a study of the shore fly *Paracoenia bisetosa* (Coquillett).

Life History

Setacera needhami is apparently confined solely to the algal mat habitat, the adults occurring both on the surface of the mats and on the lower stalks of vegetation (almost exclusively cattail, *Typha* sp.) which occasionally extrude through the mats. In the area of the Columbia Wildlife Refuge the algal mat habitat (Figs. 1, 2) is not necessarily ephemeral or even annual, but may persist through several seasons. As older growth dies it is forced to the bottom of the mat by new material. The mats show a relatively slow growth during the winter, but as the temperatures begin to rise during the early spring the mats change to a rich green and begin to expand. By late March or early April (during a mild year) the algae have taken on a fresh, green appearance as opposed to the rather drab, brown look of winter. Although only infrequent trips were made to the Refuge during the period December through early February, due to the mild climate of this area, the pools were found to contain rarely more than a thin covering of ice.

It may be the relative stability of the algal mat habitat and the mild temperatures of the Refuge which allow for the continued presence of *Setacera needhami* throughout much of the year. On warm days during the winter months, December
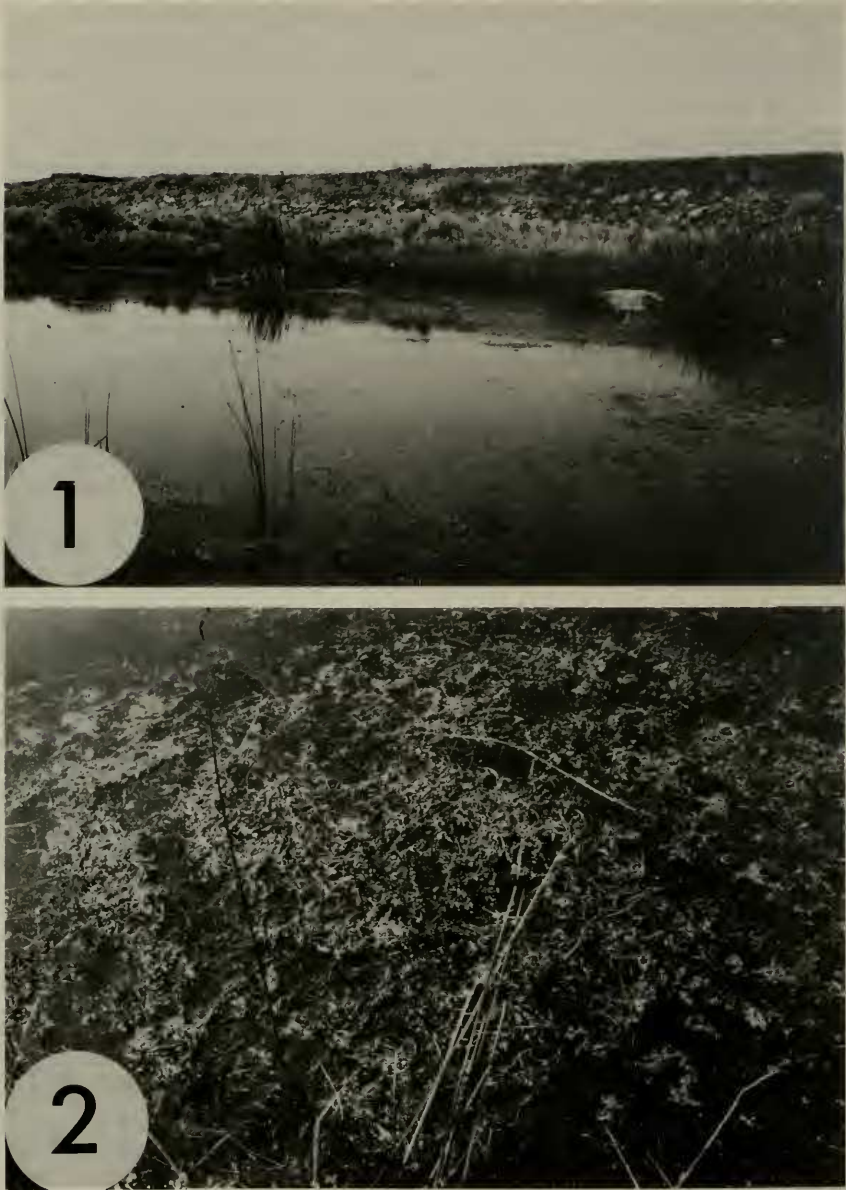
Figs. 1, 2.   Habitats of *Setacera needhami.*

through February, adults of *S. needhami* were rarely collected on algal mats and along shoreline segments of wrack vegetation. If mild temperatures (7–13°C) persisted for periods of two or three days adults could be found feeding on the algal mats.

Setacera needhami is almost always the first ephydrid to be found in the Refuge once regular collecting began in late February or early March. By late March or early April levels of both adults and immatures seemed to peak and then remained

relatively constant until late May. At this time numbers began to decline such that by early June only an occasional adult and no immatures could be located. The only stage that could be found, with some consistency, until late August was the pupa. Between mid-June and late August *S. needhami* adults were rarely collected, and then almost always singly. By late August and early September the number of adults again began to increase until population levels were as high, if not higher, than the levels in early spring. At this same time, the number of immatures located in the mats also began to rise dramatically. Population levels of *S. needhami* remained relatively high until early November when long periods of rain and/or cold temperatures seemed to coincide with their decline. A few adult females were brought into the laboratory in late October and early November, but they did not lay eggs. An examination of ovarian development was not conducted.

Besides overwintering as adults, *S. needhami* also spends the winter in the pupal stage, possibly as pharate adults. This is suggested from collections of numerous pupal cases, both empty and with fully developed adults inside, during the winter and early spring. When the mats were examined at this time only puparia were found. It is possible that pupae and/or pharate adults, still in the puparia, can overwinter in the algal mats with only minor mortality due to freezing water and inclement weather.

The previously mentioned late spring and early summer decline of *S. needhami* coincides with a rise in the level of the *Paracoenia bisetosa* population (Zack 1982, *in press*). During late summer (August and September) just the opposite occurred. That is, as the *S. needhami* population began to increase, the number of *P. bisetosa* declined. By late September and the beginning of October, *S. needhami* would again be extremely abundant on the mats while *P. bisetosa,* although common at pools which did not exhibit luxuriant growths of algae, became less noticeable. Whether any conditions existed in the mats (e.g., changes in the algal composition, temperatures, etc.) which would cause this temporal separation was not determined. How much influence, if any, each species has on the seasonal distribution of the other is unknown. I have found that the populational levels of *S. needhami* exhibit similar temporal fluctuations even in pools that did not harbor large numbers of *P. bisetosa* at any time during the year.

Occurring on the mats with *S. needhami* were the two congeners *S. aldrichi* and *S. pacifica.* Neither was found to be as abundant as *S. needhami,* and the two species combined constituted only 5–10% of the sample at any given time. All three species occurred in the same habitat at the same time and could not be separated in the field or in the laboratory until they could be examined under magnification. To assure that the individuals used in the descriptions of the immatures and puparia were *S. needhami,* I used only laboratory-reared specimens. When gravid females were brought into the laboratory, they were kept in individual oviposition chambers and each batch of eggs was placed in a separate rearing dish (Zack 1982, *in press*). The females were positively identified after eggs were laid.

The number of individuals in the field is probably regulated to a great extent by weather and to a lesser extent by predators and parasites. As was the case with *Paracoenia bisetosa* (Zack, 1982, *in press*), the level of adult *S. needhami* was drastically reduced after extended periods of rain and cold temperatures which

are common during the period March through May. Abiotic mortality factors may not affect the immatures as dramatically as the adults because of their relative protection within the algal mats. Indeed, my observations support this contention. On several occasions, after three or four days of rain I found fewer adults but could find no noticeable changes in larval numbers. Only if the mat was somehow destroyed or at least penetrated by heavy rains did the immatures seem to face the possibility of being washed from the habitat. The eggs, which are laid on top of the mats, are probably very susceptible to periods of heavy rain.

Potential predators were common in the algal mats, and several of these have already been discussed in my treatment of *P. bisetosa* (Zack 1982, *in press*). Experiments were conducted in which a few larvae were placed into an oviposition chamber containing three or four adult dolichopodids (Diptera: Dolichopodidae: *Dolichopus* spp.). Adult dolichopodids were found to feed on first and second larval instars in the laboratory. Third larval instars were also used in these tests but it was found that they were too large and cumbersome for the dolichopodids to handle. In the field I observed one *Dolichopus* sp. feeding on a second instar *Setacera* (*?needhami*) sp. Unfortunately, I did not see the predator capture the larva.

Similar experiments were conducted with dragonfly naiads (Odonata: Libellulidae) which were collected from the same algal mats in which *S. needhami* larvae were found. The dragonflies were placed into a large plastic dish and were presented with all three instars of *S. needhami,* which had been impaled on number three insect pins. Larvae were presented to the naiads by moving them back and forth approximately 2–3 cm from the naiad. The dragonflies showed a distinct preference for mature second and third larval instars, probably because of their larger size. In ten trials with each larval instar, the first was attacked only once. Likewise, recently molted second larval instars were rarely accepted (only one of ten larvae tested was attacked and eaten). Mature second and third larval instars were most frequently attacked, in some cases several times, until they were dislodged from the pin and subsequently devoured by the dragonfly.

These tests were conducted under unnatural conditions for the libellulid naiads, which were removed from their normal habitat of entangled vegetation (the algal mats) and placed into a container of water. In the habitat in which both the dragonflies and ephydrids occur, it is likely that the libellulid immatures rely almost entirely on tactile stimuli in prey capture rather than visual cues as has been recorded for most dragonfly immatures. It is improbable that the larvae of *S. needhami* can be visually observed and subesquently attacked by the naiads in the algal mat.

Predation by birds may represent only a minor factor in the overall mortality of *S. needhami* in the Refuge. While many ephydrids such as *P. bisetosa, Ephydra hians* Say, and *E. packardi* Wirth were found along the shoreline or on windrowed vegetation making them more susceptible to predation by birds, the mats on which *S. needhami* occurred were often positioned over one-half m or more of water. This location would tend to keep birds feeding at or near the shoreline, such as sandpipers and killdeers, isolated from the major *S. needhami* populations. My observations indicate that this was the case. I did make some observations, however, which indicated that surface-feeding ducks such as mallards (*Anas platyrhynchos* Linnaeus), green-winged teals (*Anas carolinensis* (Gmelin)), shov-

elers (*Anas clyeata* (Linnaeus)) and pintails (*Anas acuta* (Vieillot)) may feed on *S. needhami.* At times individuals of these birds were found feeding in or near the mats frequented by *S. needhami.* Although gut sample studies of these species were not conducted by myself, they were by Martin and Uhler (1939), who postulated that several species of ephydrids, especially those inhabiting alkaline pools, are of special importance to ducks. Although *S. needhami* is not one of the brine species, its numbers are sometimes as high as are those of the species occurring on many of the nearby brine pools.

Both adult and immature *S. needhami* were easily found in the field during the early spring and late summer. Adults occurred not only on the algal mats themselves but also peripherally on the vegetation near the surface of the water. Individuals of *S. needhami* were found on algal mats throughout the pools, often at some distance from the shore (Figs. 1, 2). In contrast, the species was rarely found along the immediate shoreline.

Immatures were located throughout the growing portion of the algal mats, many of which were five or more cm thick. They appeared to prefer the upper layers of the mat where the major algal growth occurred. The simplest and most productive means of obtaining the immatures was to sift through the vegetation by hand. Although first larval instars were difficult to locate, because of their small size, second and third larval instars were common. Using this sifting method I could usually locate three or four larvae per minute. The larvae exhibited no noticeable clumping or aggregating behavior and were never found in the decaying material at the bottom of the mats.

Eggs were rarely collected and those that were, were located by examining the mats where females were seen ovipositing. Ovipositional behavior was also observed in the laboratory. It involved the female extending her abdomen and placing an egg with the long plane parallel to the mat surface. Eggs were laid singly and in no discernible pattern. They were never inserted into the substrate but were always deposited on the surface. For three females brought into the laboratory, over several ovipositional periods, one laid 42 eggs, the second 50, and third 38. The longest-lived of these three females survived 11 days. During a single ovipositional period one of the females laid six eggs while a second laid 14.

Eggs are white when first laid and exhibit a definite sculptured pattern (Fig. 3). Within a day or two they obtain a slight pinkish-tinge, especially in a medial-transverse band. Just prior to eclosion the eggs become transparent and the developed first larval instar is visible within. Eclosion from the egg is accomplished in two to four days ($\bar{x}$ = 2.5 days; N = 52). Hatching is achieved by the larva rasping at the chorion with its mouthhooks.

Mating was observed in the field on several occasions. Precopulatory behavior is much like that observed in *P. bisetosa* (Zack, 1982, *in press*), and for *Parydra quadrituberculata* Loew and *Ochthera mantis* (DeGeer) (Deonier, 1972; Deonier and Regensburg, 1978). There appears to be little recognizable courtship behavior. In most copulatory attempts, a male simply "pounced" on another fly. In the field I recognized what I thought to be males by their slightly smaller size in relation to the females. What criteria a male uses to recognize a female are unknown. In many instances, I saw what I believed to be a male accost a second fly which also appeared to be male. In all such cases the fly was repulsed. Attempts at mating
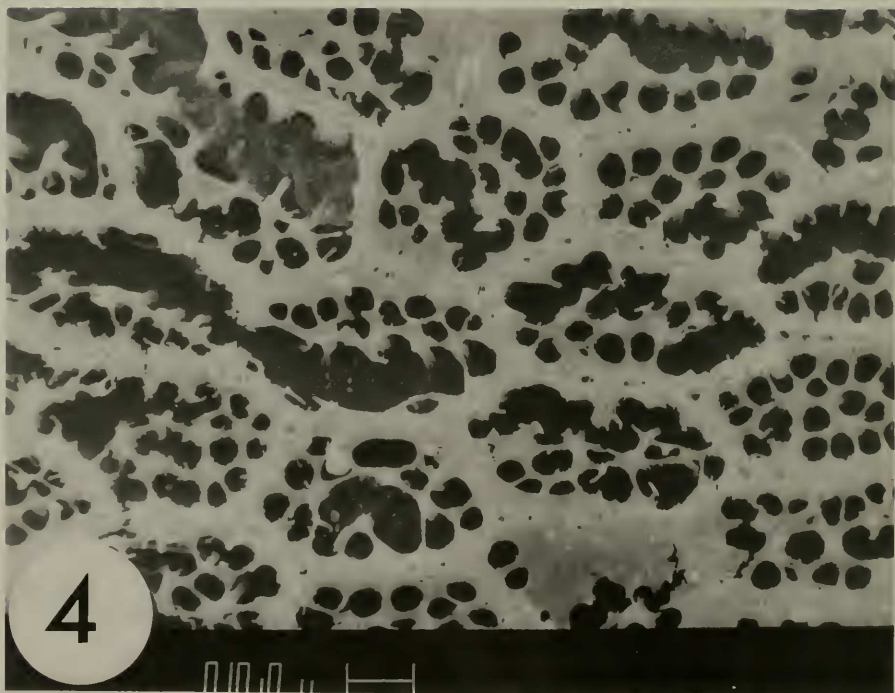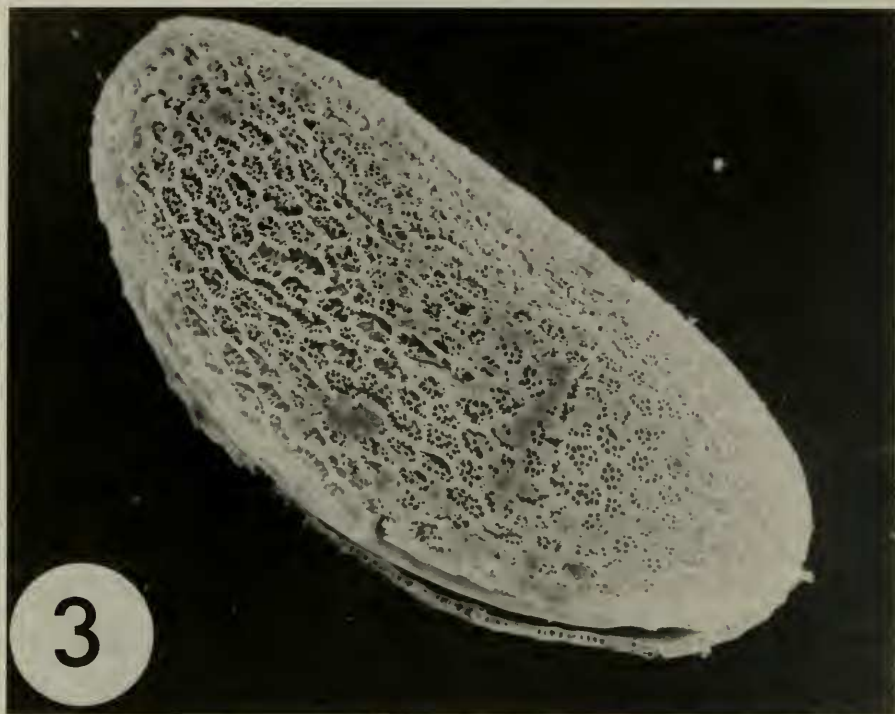
Figs. 3, 4.   *Setacera needhami.* 3, Scanning electron micrograph of egg. 4, Same, close-up of chorionic sculpturing.

were common in the field, but few are successful. In only four of 50 recorded trials did attempted mating end in success. In one case a single fly approached a second fly seven different times, each ending in failure.

In the four cases in which copulation was successful, the sequence leading to mating seemed no different than those in which attempts at mating failed. Obviously female receptivity is the ultimate factor, but the related circumstances necessary are unknown. The first step in mating apparently involves the male, jumping atop or behind a female, often jumping over her in the process. When he landed atop her, further attempts at copulation were usually discouraged by the female's scurrying-off. If a male landed behind the female, he would quickly turn and attempt to mount her from behind. If receptive, the female would spread her wings and slightly upturn her abdomen. In this way she allowed the male to mount and initiate copulation. If she was not receptive, she simply held her wings over her back or scissored them slightly to effectively prevent the male from mounting. As in the other ephydrids, the male used his forelegs to grasp the female at the bases of the wings and his mid- and hindlegs to grasp her abdomen. For the four cases in which I observed successful mating, copulatory periods ranged from 49 s to 4 min 14 s. Each of these copulating pairs were disturbed by a third individual which caused them to disengage. All observations on mating were conducted at the algal mats.

Females obtained from field-collected pupal cases exhibited premating periods of two to four days ($N = 4$). Mating did take place in the ovipositional chambers, but precopulatory behavior was not observed. Egg production records were kept for only two of the flies with 108 and 92 eggs being laid during lifetimes of 18 and 23 days, respectively. Of the remaining two females, one lived nine days while the second survived 17. For six males which had been collected as pupae in the field, the oldest survived 22 days ($\bar{x} = 14.3$ days).

In the laboratory, batches of eggs were taken from single females and placed into dishes containing agar. Five to ten of these eggs were then placed into rearing dishes supplied with a 1–2 mm thick piece of algal mat. Upon eclosion the first instar began feeding, some burrowed into the mat, while others traveled along the surface for a period of several hours. The first larval instar is covered with microsetulae which give it a rather sooty-looking appearance. However, the larvae did not seem to pick-up a covering of detritus as observed in *Parydra quadrituberculata* by Deonier and Regensburg (1978). The larvae are equipped with well developed claws on the prolegs which aid in movement through the mats. Within two or three hours all of the first larval instars were well within the vegetation and feeding. The first stadium lasted between one and three days ($\bar{x} = 2.1$ days; $N = 44$). Although I obtained cast exuviae from only the algal surface, these were few, and it is doubtful that all molting took place there.

The second larval instar was comparable to the first in appearance except that most were slightly more setulose and distinctly duskier in appearance, especially when viewed dorsally. Within one day after molting the larvae developed a distinct greenish-tinge throughout the digestive tract as they continued to feed. They were also rarely found at the surface of the vegetation and, when removed from it, they quickly reburrowed upon replacement. The second stadium lasted between two to three days ($\bar{x} = 2.4$ days; $N = 34$). Based on recovered cast exuviae, molting took place both at the surface and in the algae.

The third larval instar was very motile and could be found throughout the mats and up to 5–6 cm deep in the field. In the laboratory they were restricted by the depth of the algal material which was rarely more than 2 cm thick. As was the case in the first and second larval instars, the third was also covered with setae, especially dorsally. The third larval instar, however, probably because of its larger size, had a relatively distinct setal pattern (Fig. 15). This pattern varied considerably, especially in intensity. The pattern was relatively indistinct immediately following the molt from the second instar but darkened considerably within the first day of the third stadial period. In rare instances the pattern did not darken, and the larva was found to be lacking many of the setulae found in the normally-appearing individuals.

Most of the third stadial period was spent feeding. Gut examinations of 12 field-collected third larval instars were conducted. Most of the material in their digestive tracts was composed of broken and partially digested strands of filamentous algae. In addition there were large amounts of substance which appeared to be non-algal vegetation. This material was very common in the mats and included fallen shoreline plants and up-rooted bottom plants. Few unicellular algae were found in these samples while no diatoms were discovered. These investigations were conducted by simply opening the larva, removing the digestive tract and examining the material in it at various magnifications. A more refined study of the feeding habits may prove revealing, especially if one considers that there may be competition for preferred foods with other algal mat inhabitants.

The third stadial period lasted between 4–7 days ($\bar{x} = 5.1$ days; $N = 22$). During this time the larvae feed voraciously for the first 60–70% of the period. After feeding a larva would settle on top of the mat or just below the surface, and contract in length to about two-thirds the size of a normal larva. As in other species studied (Zack 1982, *in press*), *S. needhami* exhibited yellow pigmentation in the anterior portion of the larva by the time the post-feeding period was attained. The contracting larva would often wrap the anal proleg around a twig or another piece of vegetation in the rearing dish. At other times larvae would hold onto each other. In the field this same grasping phenomenon was found in almost all pupal cases collected and probably serves to anchor the pupal cases in the mat should it undergo a period of flooding. It may also hinder predators attempting to dislodge the pupal cases from the mat. The post-feeding period lasted from one to two days, after which time the puparium was formed. Within two or three days the first indications of the developing adult became visible through the pupal case. Eclosion occurred within six to nine days ($\bar{x} = 7.5$ days; $N = 20$).

Based on data obtained in the laboratory, the egg to adult development time of *S. needhami* ranged from 15 to 26 days. This would indicate that during an average year, in which the first adults appeared by mid-March, the species may undergo two to three generations before almost completely disappearing by early to mid-June. The period of aestivation is spent in the pupal state, it being the only stage found consistently in high numbers between the period June to early September. If eclosion from the puparium takes place in September, it is probable that *S. needhami* passes at least two additional broods, the second of which ends with overwintering pupae (pharate adults?) and adults. The adults, as an overwintering stage, may be in a state of reproductive diapause. The pupae apparently overwinter in the algal mats.
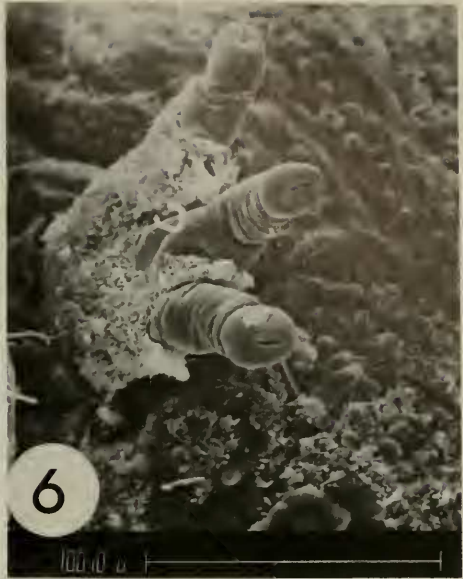
Figs. 5–8. *Setacera needhami,* scanning electron micrographs. 5, Anterior spiracle, second instar. 6, Anterior spiracle, third instar. 7, Posterior spiracle, second instar, retracted. 8, Posterior spiracle, second instar, extended.

DESCRIPTIONS OF IMMATURE STAGES

Egg (Figs. 3, 4).—Length 0.47–0.55 mm; maximum width (in dorsal view) 0.15–0.22 mm. Elliptical, more convex dorsally than ventrally. Chorion with an irregular hexagonal pattern (Fig. 4) slightly compressed anteriorly and posteriorly. Micropylar end slightly more blunt than opposite end, micropylar stalk situated in a small depression. Eggs pale white to light pink when first deposited, developing

a pink center within 12–24 h, transparent at eclosion, larva distinctly visible within.

First larval instar.—Total length 1.20–2.10 mm; main body 1.10–1.96 mm; breathing tube 0.23–0.30 mm; maximum width 0.20–0.31 mm. Integument transparent, non-patterned, larva appears bare during early part of stadium but later the fine hairlike spinulae darken and become evident. Similar to 3rd instar except in the following characters: Segment 1 bilobed anteroventrally on either side of atrial opening, each lobe bearing a group of 8–10 elongate, hairlike spinulae; antenna with 2nd lobe lightly pigmented. Segment 2 encircled by a band of fine, dark, hairlike spinulae, most pronounced dorsally and below, weak at sides; anterior spiracles absent. Segments 3–4 encircled by hairs, with a slight indication of banding on the anterodorsal margin; with occasional large, prominent, black hairs above and laterally which may be sensory in function; tubercles absent. Segments 5–11 with prolegs only slightly lobed, claws less pigmented; each segment covered with an irregular arrangement of hairlike spinulae above and laterally becoming more stout ventrally; triannulation only weakly evident beneath; a series of large dark hairs dorsally and laterally, possibly sensory in funtion. Segment 12 with posterior spiracular caps slightly pigmented, each with 2 indistinct spiracular openings which appear to be continuous, spiracular scar absent, hydrofuge lamellae short, projections greater in number, often lightly pigmented. (Based on 12 specimens.)

Cephalopharyngeal skeleton, length 0.20–0.25 mm; lightly pigmented; posterior margins of mouthhooks not broadened, more or less pointed; accessory and ligulate sclerites absent; parastomal bar free from hypostomal sclerite anteriorly; dorsal bridge only slightly broadened medially, apparently without windows; dorsal and ventral cornuae long and slender, simple (without teeth) and apparently lacking windows, slight indication of reticulation, especially on the ventral cornua; dorsal cornua slightly shorter than ventral, both more or less pointed posteriorly, ventral piece bulging slightly at middle.

Second larval instar (Figs. 5, 7–11).—Total length 2.70–3.51 mm; main body 2.61–3.57 mm; breathing tube 0.63–0.75 mm; maximum width 0.60–0.69 mm. Integument translucid, body covered with fine hairs, not patterned. Similar to 3rd instar except in the following characters: Segment 1 (Fig. 9) with oral combs less developed and less pigmented; spinose anteroventral lobes on either side of mouth opening but spines less developed than in 1st instar. Segment 2 with anterior spiracles (Fig. 5) less distinct, with 3 or 4 lobes, less pigmented, lobes not separated from one another as great distally as in 3rd instar. Segments 5–12 with bilobed and trilobed sensillae only slightly evident. Posterior spiracular caps (Figs. 7, 8) with hydrofuge lamellae less developed, each with a darkly pigmented patch medially, spiracular openings indistinct.

Cephalopharyngeal skeleton (Fig. 13), length 0.40–0.49 mm; slightly less pigmented; parastomal bars medially fused to hypostomal sclerite for only a short distance; hypostomal sclerite not fused to pharyngeal sclerite; dorsal bridge only slightly broadened medially, reticulation not as apparent; dorsal cornua long, slender, lacking toothed appearance, without windows; ventral cornua truncate, broadened posteriorly, without windows, appearing reticulate on posteriorly broadened area. (Based on 10 specimens.)

Third larval instar (Figs. 6, 12, 15, 16).—Total length (breathing tube held at
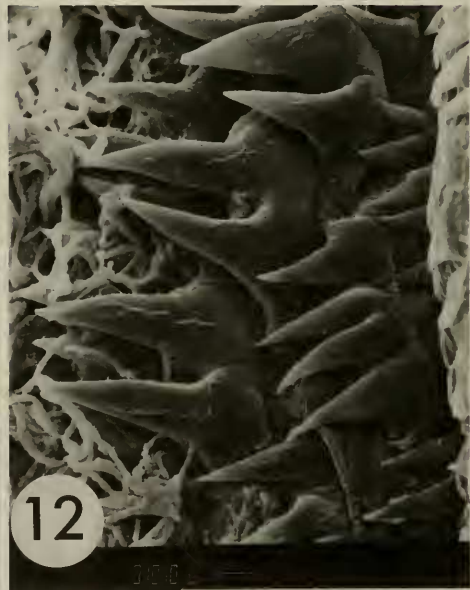
Figs. 9–12.   *Setacera needhami*, scanning electron micrographs. 9, Head segment, second instar. 10, Sensory tubercle on 8th abdominal segment, second instar. 11, Proleg on 3rd abdominal segment, second instar. 12, Spinose band on 1st thoracic segment, third instar.

obtuse angle to main body) 7.31–10.52 mm; main body 7.11–8.69 mm; breathing tube 1.45–2.03 mm long; maximum width 1.11–1.53 mm. Integument translucid; internal structures visible to some degree, posterior ½ of internal tracheal system visible; numerous spines and spinulae covering integument; dorsum patterned, varying greatly in intensity, that of segments 11 and 12 faint or more often lacking (Fig. 15). Shape fundamentally muscoid; anterior ½ tapering slightly to head,

caudal segment (12) elongate, forming a telescoping and distally branching breath-
ing tube; segments 1 and 2 retractile; prolegs present on segments 5–12, each
bearing rows of well-defined claws. Segment 1 bilobed anteriorly, each lobe bearing
an elongate 3- or 4-segmented antenna, basal and 3rd segment non-pigmented;
ventrally each lobe bearing a sensory plate. Facial mask with a pyramid-shaped
area of rows of posteriorly-facing, comblike structures anterior and lateral to
mouth opening, 1st row with 4 combs and each succeeding row with approximately
8 combs, forming a partial semicircle around the atrial opening. Prothorax (seg-
ment 2) with anterior band of spinulae (Fig. 12) in 7–9 irregular rows continuing
relatively uninterrupted to dorsolateral margin where banding ceases; dorsum
moderately spinulose, patterned, but posterolateral and posteroventral areas
essentially bare with only some slight spiculation; anterior spiracles (Fig. 6) laterad,
located at posterior border, 3 or 4 lobed, dark at tips. Mesothorax (segment 3)
with anterior band of 20+ rows of spinulae completely encircling segment, pos-
terior ⅔ of segment spinulose, more so dorsally than ventrally or laterally; segment
bearing a series of slightly raised tubercles each bearing a 3- to 4-lobed sensillum,
tubercles more evident ventrally and laterally than dorsally. Metathorax (segment
4) with an anterior band of 20+ rows of spinulae completely encircling segment,
but coalescing into heavily spinulose dorsum; posterior ¾ of segment only mod-
erately spinulose laterally and below. Segments 5–11 (abdominal segments 1–7)
variously wrinkled, but each with 3 somewhat indistinct annuli; each segment
densely covered with spinulae and patterned (Fig. 14) except for last 2 segments;
segments with an encircling pattern of tubercles arranged medially, each bearing
a 3- to 4-lobed sensillum. Prolegs present on each segment, those of segments 6–
11 subequal, that of segment 5 approximately ½ as large as others. Prolegs (Fig.
11) well-developed, bilobed, with 2 distinct rows of claws and a 3rd irregular row,
claws directed posteriorly, 4 claws/row/side, those of anterior row largest, of 2nd
row approximately ⅔ as large, and of 3rd row small, ⅓–½ as large as preceding
row; claws surrounded by spinulae which are slightly more robust than those
occurring on remainder of segment. Segment 12 (caudal) bearing an elongate
bifurcating breathing tube distally and a well-developed bilobed anal proleg ven-
trally. Each ½ of proleg with 5 irregular rows of claws, approximately 5 claws/
row, those of distal-most row largest, of proximally preceding rows progressivley
smaller, and approximately ⅔ size of those in preceding row. Perianal pad located
ventrally, subcircular, glabrous, bilobed posteriorly, furrowed by medially occur-
ring anal slit, a patch of spinulae posteromedially. Anal proleg bearing tubercles
on each side lateral to spinule patch of perianal pad, each tubercle bearing a 3-
to 4-lobed sensory papillum (Fig. 10). Segment 12 with 2 pair of well-developed
sensory papillae, most anterior pair located on large tubercles at medial (excluding
breathing tube), dorsolateral margin of segment, 2nd pair located on smaller
tubercles at anteromedial junction of breathing tube with main body. Breathing
tube with 3 pair of well-developed sensory tubercles, most proximal pair located
ventrolaterally on basal ½, 2nd pair located at middle of breathing tube, ventro-
laterally, 3rd pair located just beyond middle, dorsolaterally; tube moderately
spinulose on basal ¾, to bifurcation, branches glabrous. Posterior spiracular caps
dark amber, rounded apically, each bearing 4 suboval spiracular openings, spi-
racular scar indistinct, cap bordered basally by 4 groups of hydrofuge lamellae
each composed of 6–10 transparent hydrofuge processes.
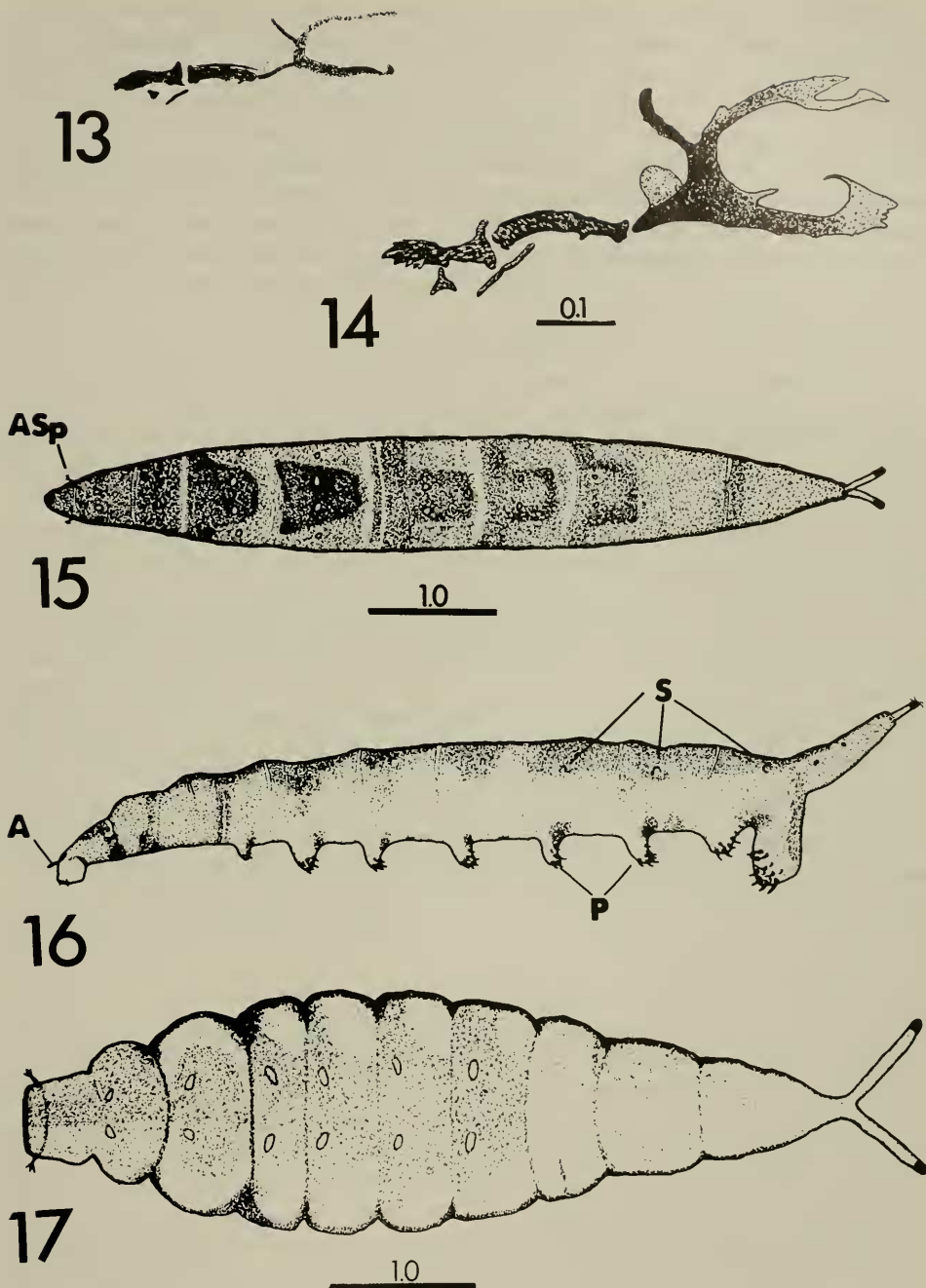
Figs. 13–17. *Setacera needhami*. 13, Cephalopharyngeal skeleton, second instar. 14, Cephalo-pharyngeal skeleton, third instar. 15, Third instar, dorsal view. 16, Third instar, lateral view. 17, Puparium, dorsal view. Abbreviations: A = antenna; ASp = anterior spiracle; P = proleg; S = sensory tubercle.

Cephalopharyngeal skeleton (Fig. 14), length 0.69–0.75 mm; amber to darkly pigmented; posterior margins of dorsal and ventral cornuae and lateral pharyngeal process dark amber, remainder black. Mouthhooks paired, not connected, non-fenestrate, length 0.09–0.11 mm; hook part of mouthhook slightly decurved, broad and spoon-shaped, sharply toothed apically with 2 elongate teeth anterodorsally, 5–6 spinelike teeth beneath, most posterior tooth slightly more stout than preceding; base broad, slightly concave and bilobed, inner lobe smaller than outer; posterior margin articulating with anterior of hypostomal sclerite, not fused. Accessory mouth sclerite located ventrolaterad to mouthhooks, roughly V-shaped. Ligulate sclerite paired, thinly rod-shaped, situated ventrad to mouthhooks and anterior to hypostomal sclerite. Hypostomal sclerite paired, length 0.19–0.21 mm; H-shaped in ventral view, consisting of 2 pair of longitudinal sclerites and 2 bridges, expanded anteriorly to articulate with mouthhooks. Anterior hypostomal bridge situated at articulation with mouthhooks, not fused to hypostomal sclerite; posterior hypostomal bridge approximately ⅔ length of hypostomal sclerite from anterior bridge. Epistomal plate broad posteriorly, with 2 large anterior teeth. Pharyngeal sclerite length 0.38–0.45 mm; ventral pharyngeal lamella with 15+ longitudinal ridges running from posteroventral margin of hypostomal sclerite to posteroventral margin of pharyngeal sclerite; forward portion not fused to hypostomal sclerite; paired lateral pharyngeal processes large, flat and rounded dorsally, fused to pharyngeal sclerite; dorsal bridge broadened medially, reticulate, with numerous windows, variously toothed at margins; dorsal cornua long and slender, variously toothed, large toothed process anterodorsally, large open window at posterior margin; ventral cornua thin, elongate, posterior margin with broken (like a snapped tree) outline, large window dorsally which may be open or closed, often varying in the same specimen. (Based on 18 specimens.)

Puparium (Fig. 17).—Total length 6.20–7.31 mm; main body 5.34–5.78 mm; breathing tube 1.36–1.82 mm; maximum width 1.40–1.97 mm. Amber to dark brown, uniformly translucid. Ellipsoidal, truncate anteriorly, tapering posteriorly into an elongate breathing tube. Venter arcuate, dorsum relatively flattened. Anterior segments 1–3 invaginated. Anterior spriacles trilobed (in most cases) arising on anterolateral margin of dorsal cephalic cap. Dorsal cephalic cap truncate anteriorly, line of weakness running dorsolaterally along segments 2–4, curving mesad and forming a transverse line along posterior margin of segment 5. Markings similar to those described for 3rd instar, varying greatly in intensity. Sensory papillae sclerotized, arranged as described for 3rd instar. Puparium, except for area posterior to bifurcation of segment 12, densely spinulose both dorsally and ventrally. Segments 5–12 each bearing ventral prolegs, those on segments 5–9 flat to weakly convex, proleg of segment 11 flat, hidden in convexity between prolegs of segments 10 and 12; lobe of segment 10 elevated, claws facing posteriorly and opposing the anteriorly-facing claws of proleg of segment 12; claws of prolegs of segments 5–9 essentially biserial with light spiculation both posteriorly and anteriorly to major spines; segments 10 and 12 multiserial, claws stronger than those on segments 5–9 and 11, segment 11 with biserial claws. Segment 12 flattened posteriorly with ovid-shaped perianal pad; pad devoid of setae, with anteriorly-facing, broadly-U-shaped convexity arising posteriorly and surrounding the anal slit, spinule patch at posteromedial border. Segment 12 elongate distally forming a breathing tube bifurcating at distal ⅔, angle of bifurcation often exceeding 100°;

large sensory tubercles on anterolateral ¼ of breathing tube; posterior spiracular caps more darkly amber than remainder of puparium, spiracular areas only faintly discernable. (Based on 15 specimens.)

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